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Exploring Visual Adaptation at High Intensity Levels with a Flash-Probe Paradigm

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14. ABSTRACT
We have studied the effect of pulsed, high-intensity, periodic backgrounds on light adaptation. For this we have used a flash-probe paradigm involving the measurement of thresholds for detecting probe stimuli presented at various phases against a modulated adapting background consisting of brief intense light flashes. We have varied the frequency of the background from 1 Hz to 64 Hz. while keeping the average intensity of the background modulation constant. We have utilized state-of-the art high-intensity white light emitting diodes to enable measurements at time-average adapting intensities greater than 106 td, several orders of magnitude higher than previous workers. The aim of the study was to investigate the temporal dynamics of light adaptation processes that occur when the eye is exposed to a train of discrete high intensity flashes of light. In addition, we attempt to draw some qualitative comparisons with existing data from the probe sinewave paradigm. Overall, despite the experimental differences, summary measures derived from the flash-probe data set are remarkably similar to those measured using the probe-sinewave technique.

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light adaptation, flash-probe, probe-sinewave, temporal dynamics, flicker

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1. Introduction

A wide variety of psychophysical paradigms have been used to study temporal effects in visual adaptation. The earliest studies used aperiodic light stimuli; brief stimuli superimposed on backgrounds of different light intensity,[1-3] while more recent studies have tended to use periodic stimuli; brief stimuli presented on modulated backgrounds, particularly the probe-sinewave paradigm.[4-7]. For the probe-sinewave paradigm the threshold for detecting a brief stimulus (the probe) is measured at various phases against a background that is modulated sinusoidally in time.

From these, and similar studies, models of light adaptation dynamics have been developed.[8-12]. In a recent review of probed-sinewave experiments investigating the dynamics of light adaptation, Wolfson and Graham (2006) challenged existing models of light adaptation dynamics with probe-sinewave data and found that the model of Snippe et al.[10,11] correctly predicts most of the probe-sinewave effects very well.

Our interest is in the temporal dynamics of light adaptation with high-intensity, periodic backgrounds. To study this, we have used a flash-probe paradigm and measured thresholds for detecting probe stimuli presented at various phases against a modulated adapting background consisting of brief intense light flashes. We have varied the frequency of the background from 1 Hz to 64 Hz. while keeping the average intensity of the background modulation constant. We have utilized state-of-the art high-intensity white light emitting diodes to enable measurements at time-average adapting intensities greater than 10^6 trolands (td), several orders of magnitude higher than previous workers. The aim of the current study was to investigate the temporal dynamics of the light adaptation process that occur when the eye is exposed to a train of discrete high intensity flashes of light. In addition, we draw some qualitative comparisons with existing data from the probe sinewave paradigm.

2. Methods

2.1 Apparatus

The experiments were performed on a custom-built, dual channel Maxwellian view light stimulator system.[13] The stimulator utilizes state-of-the-art high-brightness white light emitting diodes (LEDs)[14] as light sources and incorporates two channels of visual stimulation: one channel is used to provide both a steady background and an adapting (flash) field, while the other channel is the superimposed stimulus (probe) field. Both channels are presented in Maxwellian view along the same optical axis, and have variable field sizes from around 0.5 to 10°. The stimulator includes a photo-feedback control to monitor diode performance and linearity.

A diagram of the optical layout is provided in Figure 1. The light output from two white LEDs (Luxeon LXHL-LW5C, Philips Lumileds Lighting Company, San Jose, CA) is collimated, spatially filtered using apertures, and combined in a cube combiner. The image of the combined apertures is viewed by the subject through the wide field ocular. Changing the size of the aperture thus changes the angular subtense of each channel. The cube combiner transmits 50% of LED channel 1, and reflects 50% of LED channel 2 to the ocular. Conversely, the cube combiner reflects 50% of LED Channel 1, and transmits 50% of LED Channel 2 to the photodiode for monitoring and calibration purposes.

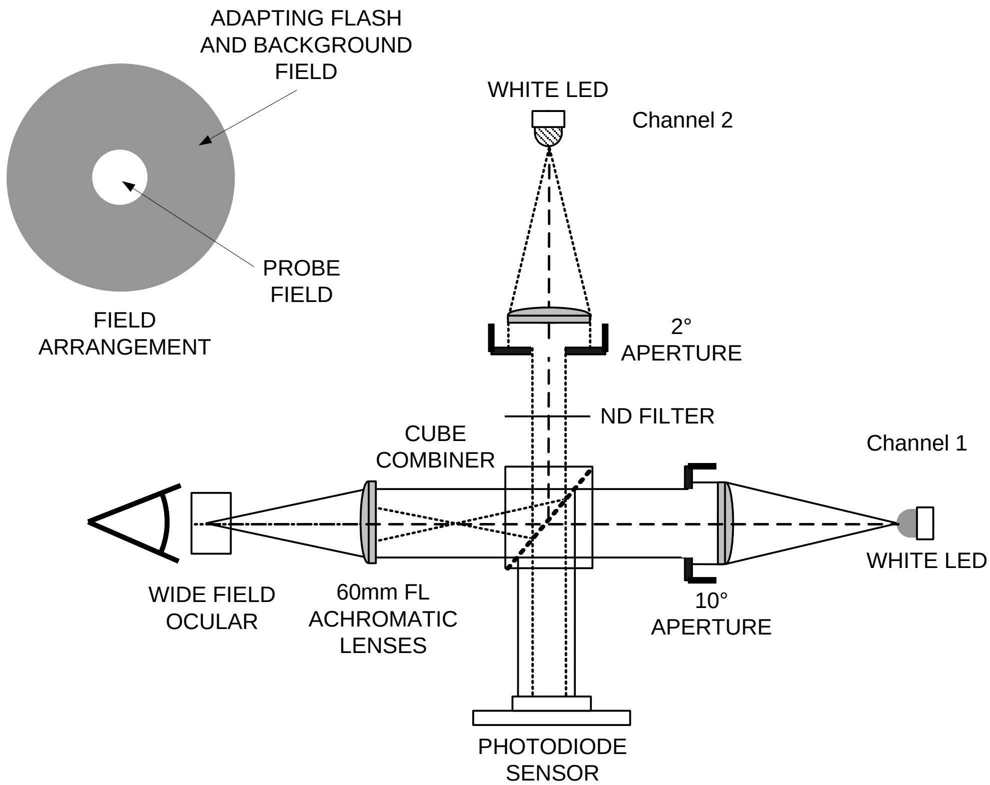


Figure 1. Optical layout of the stimulator system.

The intensity of the LEDs was controlled using a pulse density modulation technique:[15] the intensity of the adapting pulse and the probe stimulus were controlled by adjusting the frequency of 2 μs pulses The frequency of fixed current 2 μs pulses from the LEDs was varied from between 100 Hz and 40 kHz by a voltage-to-frequency converter driven through a 16 bit digital-to-analog converter card (National Instruments, DAQ) on board a Dell PC. The system was calibrated by measuring the light output from each channel as a function of the digital value from the PC, and this was used in a look-up table to compensate for any non-linearities in the system. The resulting linearity was exact within measurement error ($r^2 > 0.99$). Coarse adjustment of the dynamic range of the channels was provided by the insertion of calibrated neutral density filters in the optical train. The retinal illumination was determined using the technique described by Nygaard and Frumkes.[16]

The field homogeneity was measured with a laser beam profiler (Spiricon LBA-PC, Ophir-Spiricon Inc, Logan, UT) and was uniform to within 5%. The spectral emission characteristics of the LEDs were measured with a spectroradiometer (USB4000-VIS-NIR, Ocean Optics Inc., Dunedin, FL) throughout the pulse density range and the variation was less than 1%. The LEDs had emission peaks at 450 nm and 550 nm, and a color temperature of 5500 K.

2.2 Stimuli (the flash-probe paradigm)

The visual field arrangement used in these experiments is shown in the top-left graphic in Figure 1. The test flash (probe) subtended 2° of visual angle, and was centered on a circular field (the adapting flash and background field) subtending 10° of visual angle. Thin wires protruding just into the edge of the aperture were used to help maintain fixation and accommodation. A schematic diagram of the timing of the flash-probe cycle is shown in Figure 2.

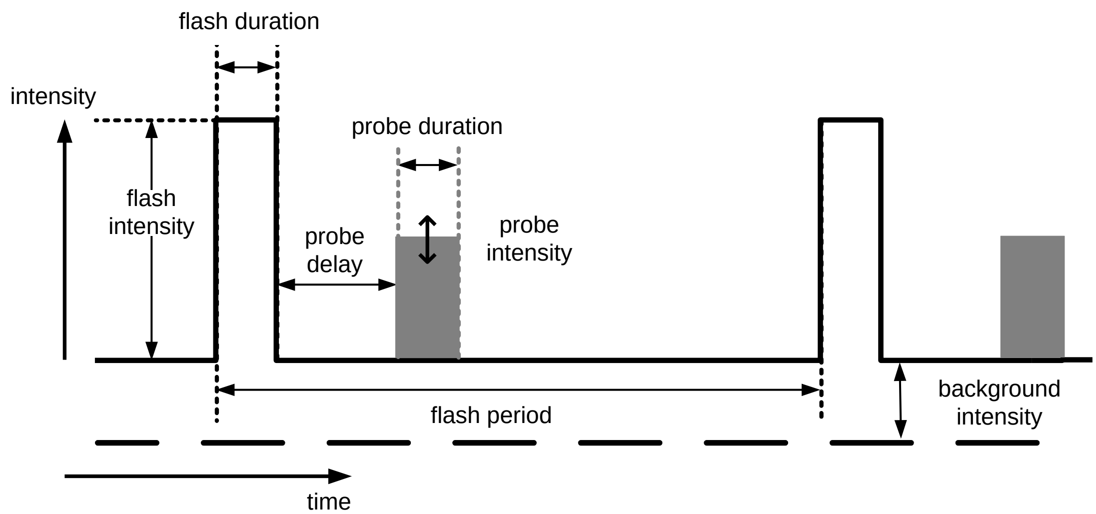


Figure 2. Schematic diagram of temporal luminance profile of adapting flash and probe stimuli.

The background field was modulated with 10 ms flashes, and thresholds were measured with 10 ms probe stimuli. Thresholds were determined for probes presented at each of eight phases (0, 45, 90, 135, 180, 225, 270, and 315°) relative to the background modulation (Figure 3), at seven adapting flash frequencies (1, 2, 4, 8, 16, 32 and 64 Hz). A phase difference of zero meant that the onset of the test pulse coincided with the onset of the test flash. The mean (time averaged) retinal illuminance of the flashes was held constant at 2.84×10^6 td, which means that the intensity of individual flashes varied from 2.84×10^8 td at 1 Hz (flash energy = 2.84×10^6 td-s) down to 4.44×10^6 td (4.44×10^4 td-s) at 64 Hz. In between the flashes the background intensity of the adapting field was 6×10^4 td. Steady state thresholds were determined with a steady background at an illuminance equal to the mean illuminance of the modulated background (2.84×10^6 td), and probe frequencies of 1, 2, 4, 8, 16, 32 and 64 Hz.

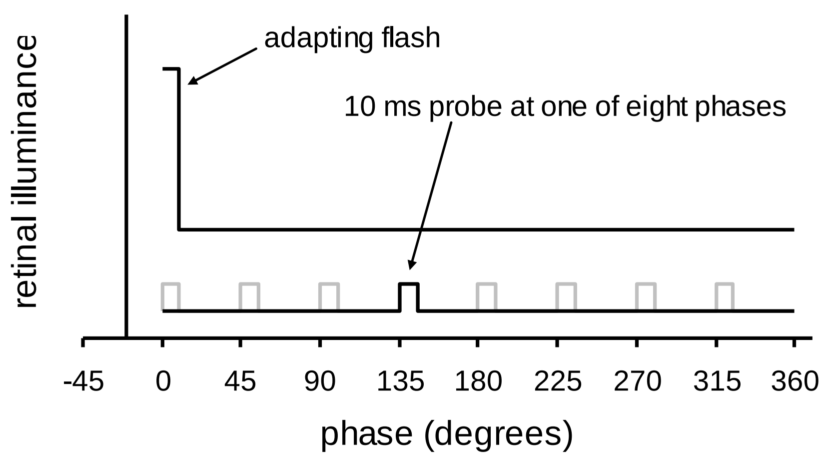


Figure 3. The temporal parameters of the flash-probe paradigm

2.3 Procedure

Probe thresholds for all eight phases at one adapting flash frequency were determined in a single session, one phase at a time. The order of the phases was different for each adapting flash frequency, and thresholds for the seven background frequencies and the steady state background were determined in random order over several sessions. At the start of each threshold determination the background intensity was set to a fixed level (6×10^4 td) and the observer aligned themselves with the optical apparatus. They were then allowed two minutes to adapt to this level. A flash-probe trial sequence consisted of a 3 s train of adapting flashes and probe stimuli, with one probe pulse for every adapting flash pulse. At the end of the 3 s sequence, a brief tone sounded and the observer responded by pressing a button if they saw the probe stimulus. After a 1 s delay the next trial sequence was presented. Thresholds were determined using QUEST adaptive staircase procedure[17] and a yes/no paradigm, with a threshold estimate being provided after twenty sequences. Before each threshold determination began, the QUEST algorithm was provided with an initial estimate of threshold based on earlier trials.

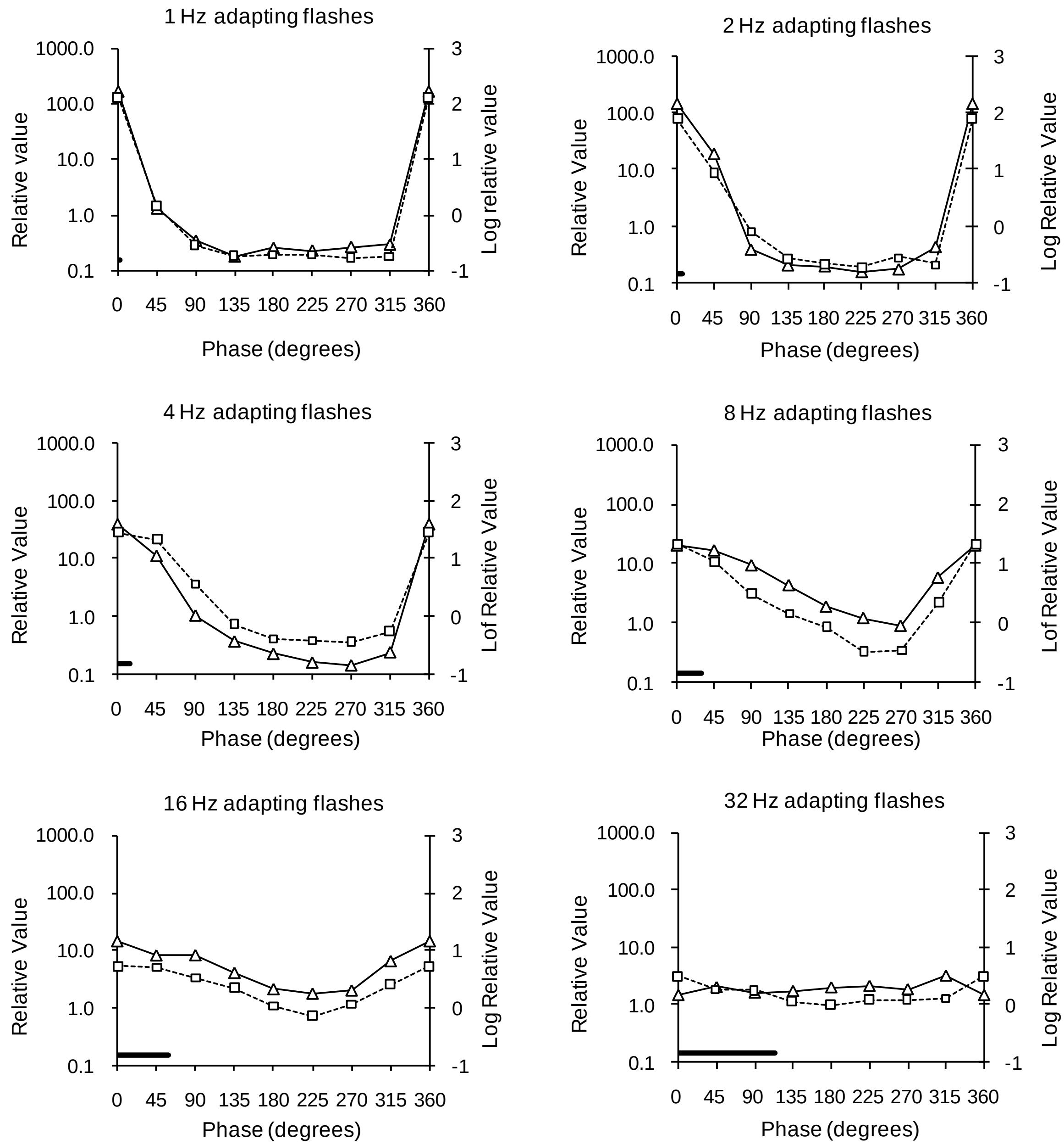
2.4 Observers

Two male observers 45 and 23 years of age (two of the coauthors) participated in this study. They had no known color defects, no paracentral scotomas, and normal dilated fundus examinations. Their uncorrected Snellen acuities were 20/20. Both were experienced psychophysical observers, and they participated in a number of practice sessions before the start of formal data collection. The voluntary informed consent of the observers was obtained as required by 32CFR219 and Air Force Instruction 40-402.[18]

3. Results

Probe thresholds were expressed as relative probe thresholds, calculated as the probe threshold luminance on the modulated background divided by the probe's threshold luminance on the steady-state background at an illuminance equal to the mean of the modulated background. Probe thresholds calculated in this way are plotted as a function of phase in Figure 4. Each panel in Figure 4 shows the relative threshold vs. phase relationship at a single adapting flash frequency for the two subjects that participated in the study. The black bar at the bottom of each panel shows the phase angle occupied by the 10 ms adapting flash at the given modulation frequency, indicating the portion of the cycle that the adapting flash is on.

Since the data are expressed relative to the steady state thresholds obtained with the probe on a steady background, a value greater than unity means that the threshold is higher than the steady state threshold while a value less than unity means the threshold is lower than the steady state threshold. Notice that despite small differences, the data patterns over all seven panels are very consistent across the two subjects. At low frequencies (less than 8 Hz), thresholds are higher than steady state values for only a small portion of the cycle, around the time of the adapting flash, and then for a short time beyond the offset of the flash. In between, during the off phase of the adapting flash cycle, thresholds fall to below steady state values. Overall, the variation of probe threshold with phase is asymmetric and peaked.



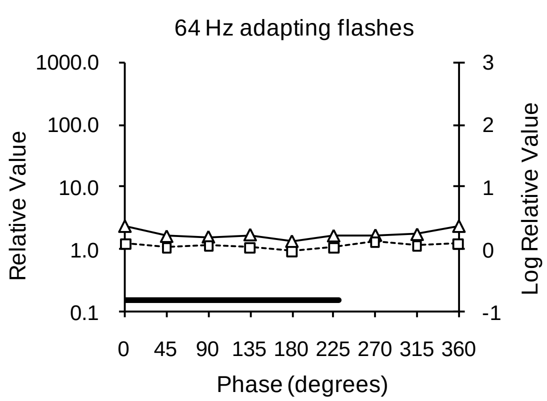


Figure 4. Each panel shows the relative probe threshold for two observers as a function of the phase of the adapting flash sequence. Each panel shows a different frequency of modulation. The black bar at the bottom of each panel shows the phase angle occupied by the 10 ms adapting flash at the given modulation frequency (i.e. “on time”).

As the flash frequency is increased, thresholds become more elevated throughout the cycle, to the extent that they do not fall below the steady state levels (i.e. relative values are >1.0) even during the off phase of the adapting flash cycle. Also, especially at 8 and 16 Hz, thresholds late in the cycle become more elevated, even though these thresholds are measured in the off phase, before the onset of the next adapting flash. Overall, the variation in probe threshold with phase is more symmetrical, and the variation in probe threshold across the cycle is reduced (i.e. the curves are flatter). For each data set, at each frequency (i.e. for each panel in Figure 4), following the approach used by Wolfson and Graham[7], the summary measures log dc-level and log peak-to-trough distance were derived (see Figure 5**).**

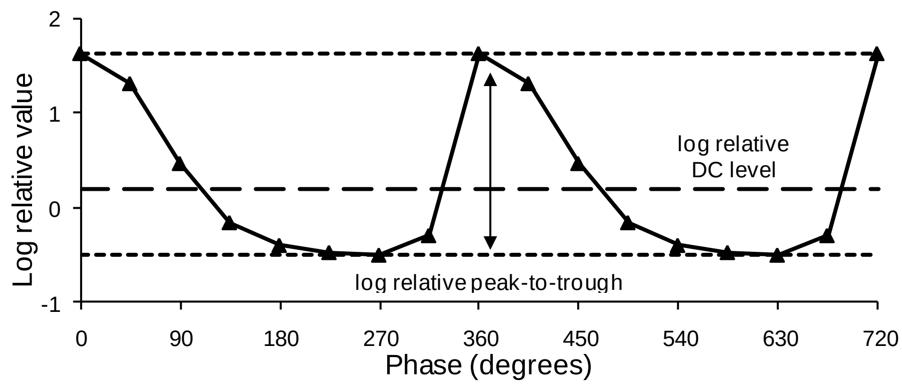


Figure 5. Derivation of summary measures.

The log form of the dc level was calculated as the average of the log relative probe-threshold values at the different phases while the log form of the peak-to-trough distance was calculated as the difference between the maximum and minimum values (across phase) of the log-relative probe thresholds. Linear forms of the relative probe thresholds were also calculated.[7] These summary measures, averaged across the two subjects, are plotted as a function of the adapting flash frequency in Figure 6 and Figure 7.

The dc component represents the unmodulated component of the threshold elevation produced by the flickering background. It is described by the log and linear dc-level curves, and the level of this dc-component varies with the adapting flash frequency (Figure 6). In the log form, it is lowest for low frequencies, and rises as the frequency increases, reaching a peak at around 8-16 Hz, and then falling off again as the frequency is increased to 64 Hz. The peak value is around 0.56 log units at 16 Hz, which means that the dc level is elevated by a factor of over 3½ times compared with against a steady field at the same average luminance. In the linear form, the dc component decreases as the flash frequency increases.

The magnitude of the difference between the peak to trough threshold provides a measure of the extent to which the background modulates (induces variations in) the probe threshold (Figure 7). In both the log- and linear forms, this measure starts with a high value at low frequencies and declines steadily with increasing frequency up to 32 Hz, where it approaches the steady state threshold and flattens.

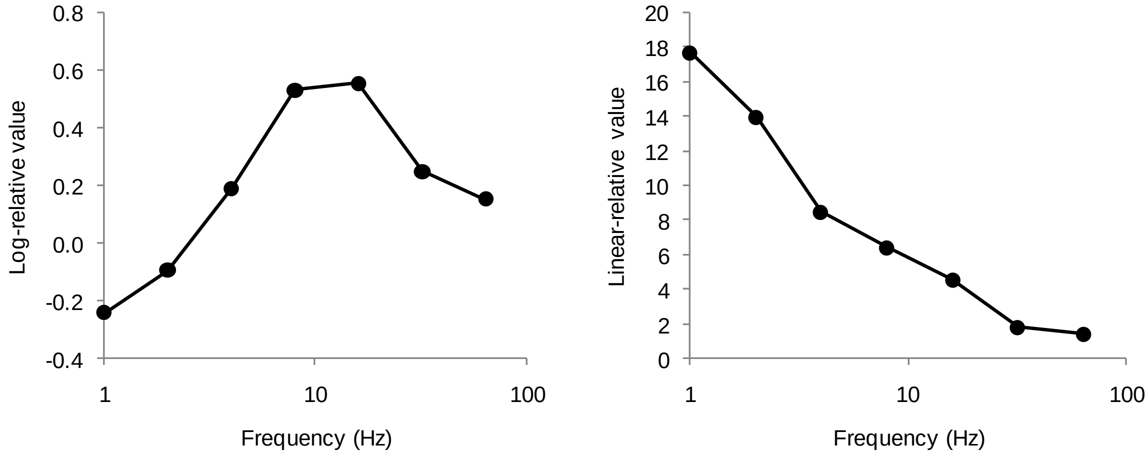


Figure 6. Log and linear dc level measures derived from relative probe threshold versus phase curves, averaged over two observers.

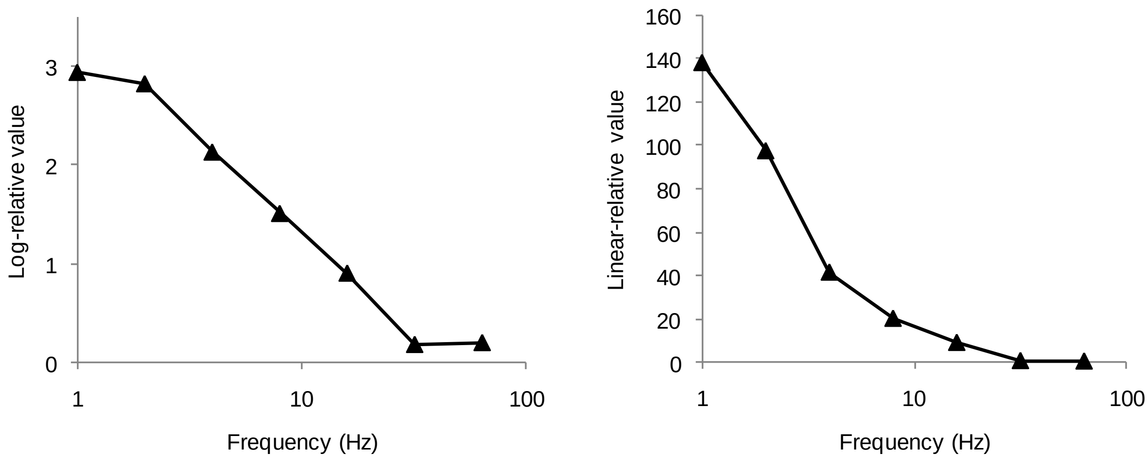


Figure 7. Log and linear peak-to-trough measures derived from relative probe threshold versus phase curves, averaged over two observers.

4. Discussion

The visual system does not adjust to changes in light instantaneously, but rather goes through a process known as light adaptation, which occurs in order to adjust to naturally occurring changes in illumination. For the cone system, the dynamic range over which this adaptation occurs covers nine orders of magnitude, from 10^{-3} $cd \cdot m^{-2}$ to more than 10^{6} $cd \cdot m^{-2}$. This is achieved through a combination of slow and fast gain controls, which maintain sensitivity to small luminance differences throughout this luminance range. The processes involved in adaptation may occur in the retina and in the visual cortex (for reviews see Hood & Finkelstein[19] and Shapley & Enroth-Cugell[20]). Research has been targeted at a full understanding of the temporal dynamics of these adaptation processes; at least to the extent that the processes can be modeled with sufficient accuracy, to serve as input to models of higher-level visual processes.[8]

Historically, to investigate temporal effects in light adaptation, both aperiodic light stimuli,[1-3] and periodic stimuli,[4,21-23], including the probe-sinewave paradigm,[5,6,10,24-26] have been used.

These studies have both driven the development of, and challenged, computational models of visual adaptation; often a model based on one paradigm was not able to predict the results of another.[8] In a recent review of probe-sinewave studies, Wolfson and Graham[7] tested existing models of light adaptation dynamics with probe-sinewave data. They concluded that the model of Snippe et al.[10,11] was most attractive, primarily because it correctly predicts most of the probe-sinewave effects very well.

Figure 4 shows how the increment thresholds (as measured with a probe stimulus) vary in the presence of the flashing adapting background. At low frequencies the threshold varies with position in the flashing cycle, rising and falling roughly in phase with the adapting background. At the very low frequencies – 1 and 2 Hz, the very large and fast recovery processes taking place in the human visual system are remarkable, with over three log units of recovery (a factor of over 1,000) taking place within a half a second. However, as the frequency increases, the depth of the modulation decreases, and more or less disappears at frequencies at or above 32 Hz. Boynton[4] used a similar paradigm with a square wave modulated adapting background and two test frequencies; 15 Hz and 30 Hz. Even at 30 Hz, he found that thresholds were higher when presented during the light phase of the flash compared to the dark phase of the flash, and both were higher than those presented against a steady background.

The summary measures in Figure 6 reveal how the log dc measure describes a “band pass” system, rising to a peak at around 8-16 Hz and decreasing on either side. The linear dc data do not follow the same behavior, but appear “low pass”, decreasing steadily with increasing frequency. The reason for this is the very strong peak at phase zero at the lowest frequencies, which is compressed in the log average thresholds, but not in the linear average thresholds. Both peak-to-trough measures on the other hand (Figure 7) describe a “low pass” system.

In their recent review Wolfson and Graham[7] presented and compared existing data from probe-sinewave studies. They found that inexplicable discrepancies between the result from different research groups and different set ups were minor. Using the results from previous workers they derived the summary measures and used these to compare results, and these showed a remarkable constituency between studies. They also provided an auxiliary file containing the data sets for future researchers to use. Using these data, we plotted the results of our study together with the data sets Wolfson and Graham[7] classified as “high contrast backgrounds (photopic)”, these being methodologically most close to our study. These results are plotted in Figure 8 and Figure 9.

The comparison with probe-sinewave data provides several noteworthy observations. Firstly, the log relative dc level data obtained with the flash-probe paradigm are qualitatively and quantitatively similar to the probe-sinewave data. The log relative peak-to-trough data are not quantitatively similar, although qualitative similarities are apparent.

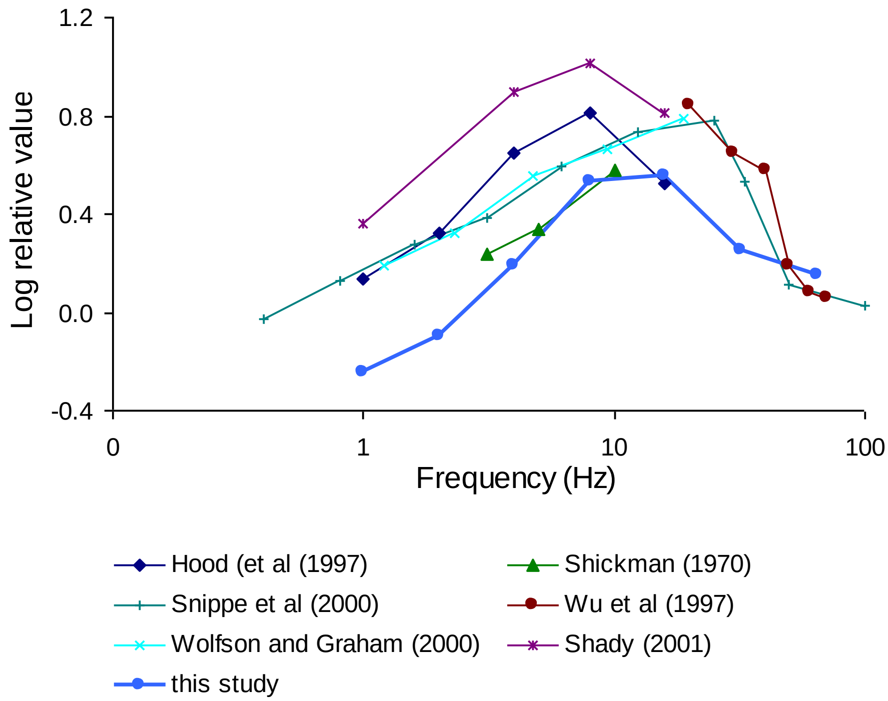


Figure 8. Comparison of the summary measure log relative dc level as a function of the adapting background temporal frequency with data collected using the probe-sinewave paradigm.

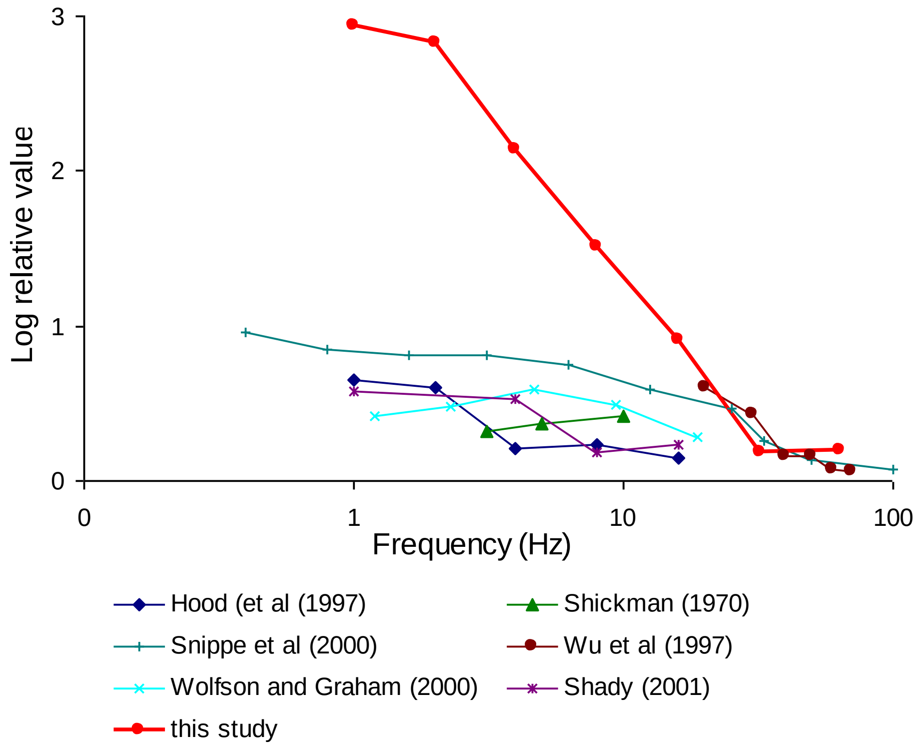


Figure 9. Comparison of the summary measure log relative peak-to-trough as a function of the adapting background temporal frequency with data collected using the probe-sinewave paradigm.

Within the log relative dc level data set, there is a subtle difference between our data and the probe-sinewave data. For probe-sinewave data the log relative dc level does not extend below zero, whereas for the flash-probe data values below zero were observed at the two lowest frequencies used, 1 Hz and 2 Hz. While log values above zero show thresholds that are elevated relative to the steady state, log values less than zero mean that those thresholds were lower than the steady state threshold. For the probe-sinewave data this would ordinarily be interpreted as facilitation. However, it may be due to other causes, because it is not seen in the linear threshold data. This observation is supported by the fact that the thresholds at 1 and 2 Hz remain well above Weber threshold levels of the steady state background presented between flashes.

The term masking refers to an interference in the perception of one stimulus (the target) by the presence of a second stimulus (the mask), that is nearby in time and space. The mask can appear before, after, or simultaneous with the target, and these temporal sequences are termed forward, backward, and simultaneous masking. Masking is a fast process distinguished from other visual interactions by its restricted time course. An interference with a longer time course is usually called adaptation.

In the present study, at 1 Hz the adapting pulse train cycle consists of a brief (10 ms) bright (2.84×10^8 td) flash, followed by 990 ms of exposure to the inter-pulse background intensity (6×10^4 td). At 2 Hz the flash is followed by 490 ms of exposure to the inter-pulse background intensity, and at 4 Hz the interval is 240ms. One possibility is that at low flash frequencies the long interval allows for fast masking processes to be complete and for slower dark adaptation processes to take place, allowing for a greater recovery of sensitivity before the next flash. In comparing the probe-sinewave studies with studies using aperiodic stimuli, Hood et al.[5] also noted that the results from both paradigms suggest that the processes in light adaptation can involve both relatively fast and relatively slow mechanisms. The fast processes are responsible for the peak-to-trough probe threshold modulations that exist even at high frequencies, while the slow processes are responsible for the change in the dc level with the flash frequency.

The low pass behavior of the linear dc level (Figure 6), which is contrary to the band-pass behavior obtained previously for sinusoidally modulated backgrounds, may be attributable to two causes. First, for sinewave adapting backgrounds at fixed contrast, the temporal gradient of the sinewave is proportional to the frequency, and becomes lower at lower frequencies. For the brief flash pulses used in the current study, the temporal gradients remain sharp, and the temporal derivative operations (band pass or high pass filters) that tend to suppress the impact of low modulation frequencies for sinewaves, would be absent. Also, the contrast (amplitude of modulation) in sinewave experiments is frequency independent. In our experiments, the contrast is highest for the lowest frequencies – with each halving in the frequency of the flashes, to keep the time-average luminance constant, the flash intensity was doubled. This would enhance the effects of low modulation frequencies compared to the sinewave experiments. It might also explain why, at low frequencies, threshold values were lower than steady state - the high peak intensity is causing some saturation and thus the elevation in dc level is lower than expected.

Although the log relative peak-to-trough shows the same low-pass behavior as probe sinewave data (Figure 9), at low frequencies the relative values in the current study are much higher than with probe sinewave data. The reason for this is most likely related to differences in the amplitude of modulation between the two studies. With the probe-sinewave paradigm the maximum and minimum luminance levels for the adapting field do not change with frequency, whereas with our paradigm the maximum luminance halves with each doubling in frequency. To compensate for this, we normalized the relative peak to trough values by dividing by the ratio of the peak intensity to the peak intensity that would be required at 50 Hz (i.e. a square wave). These are plotted in Figure 10, and show that when the relative peak intensity is taken into consideration, then the data from the current study become both qualitatively and quantitatively similar to the probe-sinewave data.

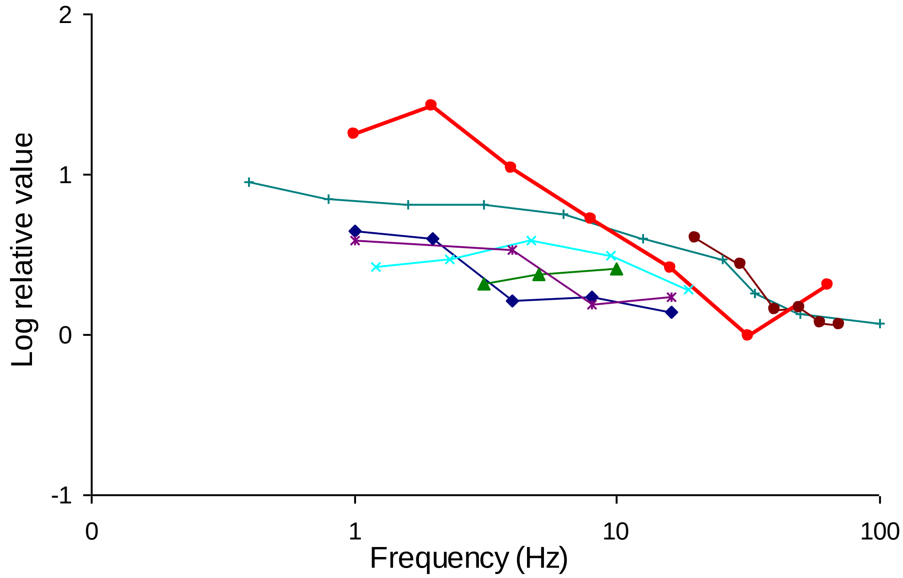


Figure 10. Comparison of the summary measure normalized log relative peak-to-trough (red line) as a function of the adapting background temporal frequency with data collected using the probe-sinewave paradigm (legend as in Figure 8).

5. Summary

The aim of the current study was to investigate the temporal dynamics of the light adaptation process that occur when the eye is exposed to a train of discrete high intensity flashes of light and to extend prior research using periodic and aperiodic stimuli in two ways; by increasing both the mean luminance and the periodic contrast. An additional aim was to compare the results using this paradigm with existing data from the probe sinewave paradigm.

We found that thresholds during the flash train appear to be dependent on two factors: the temporal proximity to an adapting flash, and the history of prior exposure to light. Thresholds are highest at the time of the adapting flash and they are elevated for a short time around the flash due to masking processes. At low flash frequencies, sensitivity after the flash returns remarkably quickly, with over three log units of recovery taking place within a half a second. As the flash frequency is increased, visual recovery between the flashes is incomplete, the level of light adaptation increases, and overall sensitivity is reduced.

Overall, the trends in the summary measures derived from the flash-probe data set are remarkably similar to those from other laboratories measured using the probe-sinewave technique,[7] which is a substantially different paradigm. Despite the experimental differences the summary measures are consistent with the existing probe-sinewave data. With both, as the modulation frequency of the high contrast background increases, the log relative dc level is bandpass, while the log peak-to-trough distance is lowpass. This study, therefore, supports the observation of Wolfson and Graham,[7] that pulses with steep onsets and offsets tend to produce results similar to sinewave data.

Early models of light adaptation were designed to either fit the data from aperiodic light masking experiments or from probe-sinewave experiments. The model introduced by Wilson[12] modified by Hood & Graham[27] and Snippe, Poot, & van Hateren[10,11] have been shown to be able to fit both sets of results.[7] The latter model has previously been regarded as most attractive because it predicted most of the probe-sinewave effects very well.[7] While we have not explicitly tested this model with our data, the striking similarity of our data with the probe-sinewave data suggest that the same model would, by implication, capture the main features of the flash-probe data.

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